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Description of *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) Paralarvae with Evidence for Spawning in Hawaiian Waters[1]

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ABSTRACT: Paralarvae of the commercially important squid *Ommastrephes bartramii* are described, and particular attention is paid to the chromatophore patterns. These chromatophore patterns are compared with those of *Stenoteuthis oualaniensis* and *Hyaloteuthis pelagica*, two other local ommastrephids with similar patterns. Limited data on spatial and temporal distributions of the paralarvae are also presented. Paralarvae of *O. bartramii* have been found at several localities along the Hawaiian Archipelago between Oahu and Midway Islands. In 1986 *O. bartramii* probably spawned in southern Hawaiian waters around the island of Oahu from, at least, the latter part of February through March. During April 1979 and April 1984 the absence of paralarvae from these same waters suggests that either the spawning period terminated earlier or the squid did not spawn as far south as in 1986. High abundances of *O. bartramii* paralarvae in some April 1979 samples suggest that spawning was more intense in the northwestern half of the Hawaiian Archipelago.

Ommastrephes bartramii is broadly distributed throughout the subtropical and temperate waters of the world's oceans. In the Pacific the northern and southern populations are discontinuous (Wormuth 1976). The North Pacific population is spread across the open ocean, where it is fished with jigs and drift nets over much of its range. The current catch is estimated to be about 300,000 metric tons/yr (Ignell, in prep).

Kubodera (1986) considered the North Pacific population of *O. bartramii* to be subtropical and to exhibit a northward feeding migration that reaches the subarctic boundary during summer, then reverses in the fall, with spawning occurring in the winter to early spring in the southern part of the Kuroshio Current.

The data of Murakami et al. (1981) on the distribution of mature *O. bartramii* suggest the possibility of three spawning regions in the North Pacific: one at ca. 140–150° E long., one at ca. 170° E long., and one between 160–180° W long. Additional evidence for the first site has been provided by Nakamura (1988) based on the distribution of mature females and by Okutani (1968) based on the presence of paralarvae.

In spite of the economic importance of this fishery, paralarvae have never been fully described, and information on their distribution is sparse. Various stages of *O. bartramii* paralarvae have been described by Naef (1923), Okutani (1965, 1968, 1969), and Nesis (1979), but the critical chromatophore patterns have been largely ignored. In this paper we describe paralarval stages of *O. bartramii* found off the Hawaiian Islands and present limited information on their temporal, vertical, and horizontal distribution in Hawaiian waters.

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MATERIALS AND METHODS

The island of Oahu has been most heavily sampled for cephalopod paralarvae. Plankton net samples have been taken off Oahu in 19–21 December 1983, 7–9 April

1984, 10–12 August 1984, 20–24 October 1984, 6–13 September 1983 (National Marine Fisheries Service [NMFS]), 16–19 December 1985 (NMFS), 22–30 March 1986, and 8–18 April 1986 (NMFS). Tows varied in net size (1–4 m^2), angle of tow (horizontal versus vertical), and depth (surface to 400 m). The samples are not strictly comparable, but during most cruises the water column was sampled from the surface to at least 200 m.

The most extensive set of plankton samples was taken during March 1986 with the 4-m^2 net. During this cruise most samples came from 11 km offshore of leeward Oahu where the bottom depth was about 2000 m. One 24-hr series, the "inshore" series, was taken, however, at 3 km from shore over depths of 500 m. One series of horizontal plankton tows was made during the cruise at the offshore (i.e., 11 km) station near the surface. The net was attached to floats and towed well behind the ship while the ship slowly turned. As a result the net filtered water between 1 and 3 m in depth and out of the direct wake of the ship. One tow was taken each hour for 23 hr.

The vertical distribution of plankton at several localities off Oahu was examined by G. Boehlert of the National Marine Fisheries Service, Honolulu Laboratory, in April 1986. He divided the upper 200 m of the water column into eight depth zones (five in the upper 100 m), which were sampled with a 1-m multiple opening/closing MOCNESS system (see Wiebe et al. 1976). In addition, surface neuston tows were taken.

The discovery of *O. bartramii* paralarvae in the March and April (1986) samples prompted our reexamination of samples taken from 12 to 28 April (south–north) 1979 along the length of the Hawaiian Archipelago. This series utilized standard 0.7-m-diameter bongo nets towed obliquely to about 200 m. Mesh size was 183 μm and volume filtered was ca. 1000 m^3 per net tow. Single daytime tows were taken about 50 km to either side of the midline of the Hawaiian Ridge. The five localities examined here were off Midway, Laysan, French Frigate Shoals, Nihoa, and Oahu. Adult *O. bartramii*, males and females, are rarely encountered off Oahu, but they have occasionally been captured by jigging and gill nets from the FTS *Hokusei Maru* during cruises in southern Hawaiian waters during late January and early February.

RESULTS

Descriptions of Paralarvae

GENERAL DESCRIPTION. The following descriptions of *O. bartramii* paralarvae are based on the specimens illustrated except for the smallest specimen. Terminology is defined in Figure 1. Chromatophores at the anteroventral margin of the mantle are either on the external surface of the mantle slightly posterior to the margin (= exterior chromatophores) or on the internal surface of the mantle and in contact with the margin (= interior chromatophores). Chromatophores on the arms and buccal region were difficult to count and are not included in the following descriptions.

About 1 mm mantle length (ML) (hatchling with yolk). The single specimen examined at this size was damaged. *Proboscis*: narrow (0.14 mm), short (the center of the tip did not reach past the tip of the arms); the terminal "disc" was folded in half; lateral "disc" suckers about half again as large as the adjacent suckers. *Chromatophores*: mantle: four midmantle, more dorsally possibly due to damage; one posteroventral.

1.6 mm ML (Figure 2A). *Proboscis*: short, strongly contracted, directed ventrally; lateral suckers nearly twice the diameter of the adjacent suckers. *Arms*: I and II with a single large sucker on each; III and IV not detectable. *Chromatophores*: ventral head: single large posterolateral pair; dorsal head: posterolateral pair large, dark; anterolateral pair faint, anteromedial large, dark, posteromedial absent; mantle: eight large midmantle; single, large posteroventral mantle; fin: one middorsal.

3.1 mm ML (Figure 2B). *Proboscis*: lateral suckers about twice the diameter of adjacent suckers; about 20 knobs on inner whorl of outer chitinous ring of large lateral suckers and about 10 knobs in this location on medial suckers (Figure 3). *Arms*: III slightly shorter than I; IV very small. I–III with basal sucker

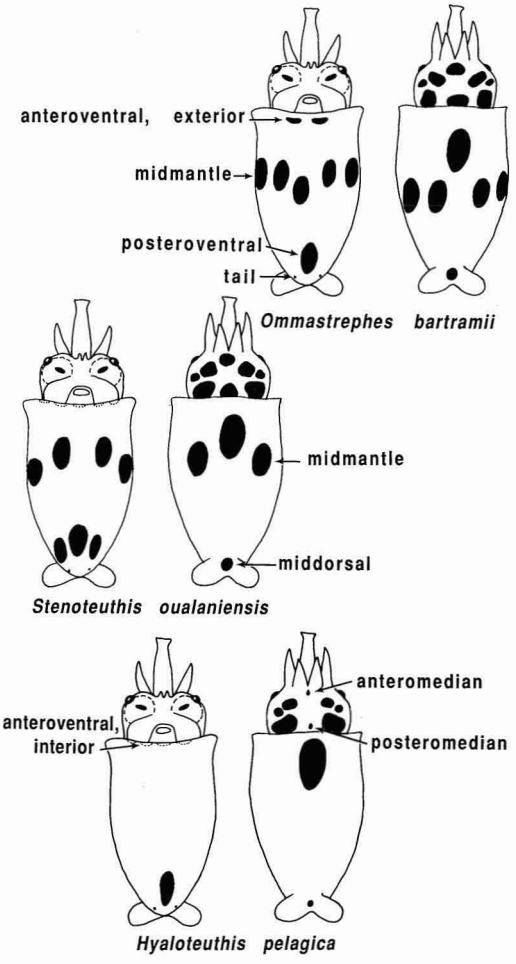

FIGURE 1. Typical chromatophore patterns in a schematic illustration of 3-mm paralarvae of each of the three species. The chromatophores have been superimposed on the same illustration to emphasize the pattern. Terminology used for chromatophore fields is defined in text.

distinctly larger than the rest. *Digestive gland*: deeper than long, with ink sac extending over posterior end; abuts cephalic cartilage. *Chromatophores*: head: eight dorsal, one pair posterolateral. Mantle: two anteroventral margin, exterior; eight midmantle; one posteroventral; one small pair "tail"; fins: one middorsal.

4.3 mm ML (Figure 2C). *Proboscis*: no split in base; lateral suckers about twice diameter of adjacent suckers. *Arms*: III equals I; IV much smaller. *Digestive gland*: same as previous. *Chromatophores*: head: eight dorsal, one pair posterolateral, three ventral. Mantle: 2 anteroventral margin, exterior; 3 anteroventral margin, interior; 19 midmantle; 1 posteroventral mantle; 1 pair (small) "tail"; fins: 1 middorsal between fins.

6.2 mm ML (Figure 2D). *Proboscis*: broad split in base; about equal to arm III in length; lateral proboscis suckers about twice diameter of adjacent suckers. *Arms*: IV small, reach level of basal suckers of III. *Digestive gland*: same as previous but slightly posterior to cephalic cartilage. *Chromatophores*: head: 12 large and 8 small, dorsal; 1 pair posterolateral; 8 ventral. Funnel: two tiny. Mantle: 3 anteroventral margin, exterior; ca. 12 anteroventral margin internal; ca. 63 midmantle; 2 posteroventral mantle; 1 pair (small) tail; fins: 1 middorsal.

12.5 mm ML (Figure 2E). *Proboscis*: absent (tentacles separated); tentacles shorter than arms IV, clubs not expanded, numerous sucker buds. *Digestive gland*: depth equals length, therefore circular in side view; well posterior to cephalic cartilage; ink sac extends nearly full length of digestive gland. *Chromatophores*: numerous; primary chromatophores mostly not clearly recognizable, numerous chromatophores present on head, mantle, arms, tentacles, funnel, and fins.

CHROMATOPHORE VARIABILITY AND COMPARISONS WITH OTHER OMMASTREPHIDS. Chromatophore patterns generally provide the easiest method for specific identification of paralarval squids (Young and Harman 1985). Harman and Young (1985), however, did not rely heavily on chromatophore patterns in identifying Hawaiian ommastrephid paralarvae because their specimens had suffered considerable damage during capture. Specimens examined in the present study are in better shape, and a more careful analysis of chromatophore patterns is possible. For comparison we have also reexamined the paralarval chromatophore patterns of the two other ommastrephids that occur in Hawaiian waters (*Stenoteuthis oualaniensis* and *Hyaloteuthis pelagica*) whose patterns are most similar to those of *O. bartramii*.

Freshly captured ommastrephid paralarvae

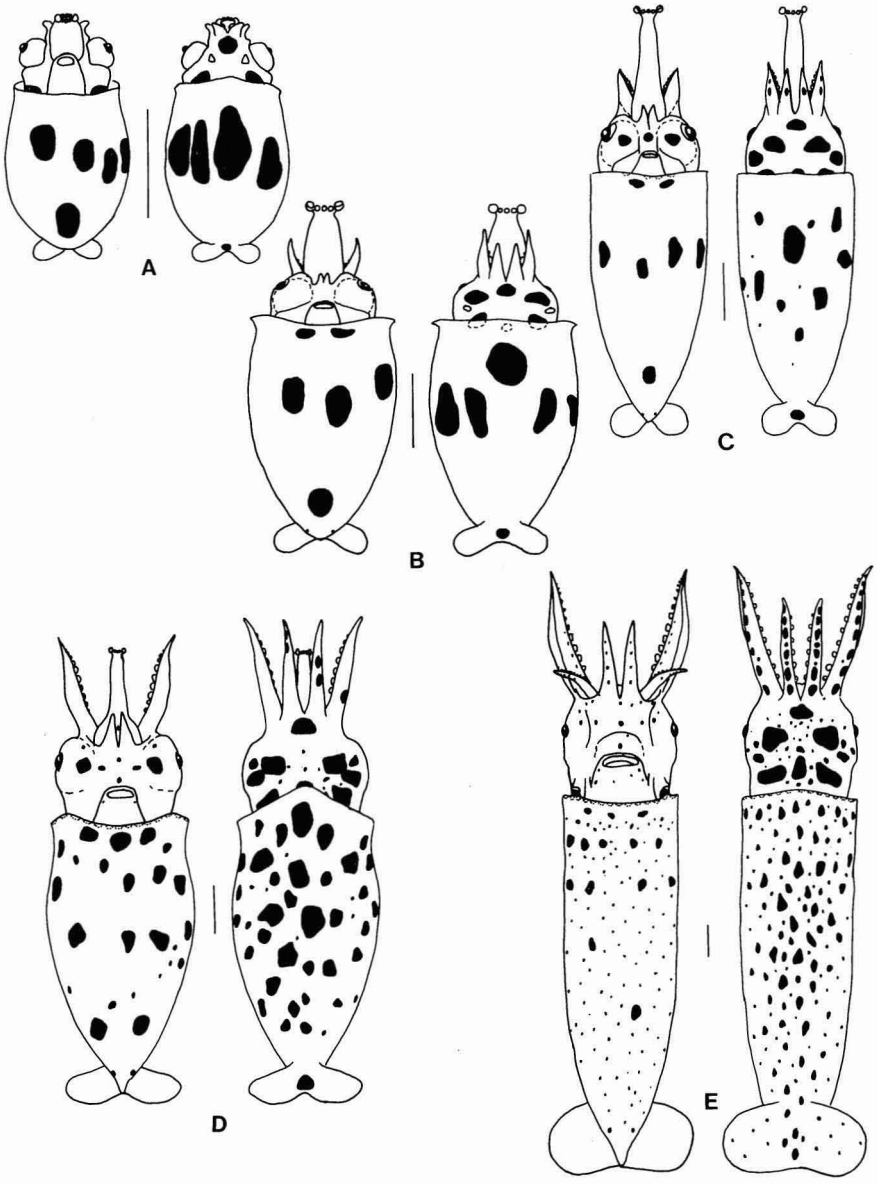

FIGURE 2. Paralarvae of *Ommastrephes bartramii*: *A*, 1.6 mm ML; *B*, 3.1 mm ML; *C*, 4.3 mm ML; *D*, 6.2 mm ML; *E*, 12.5 mm ML. Chromatophore pattern is approximate. Bar = 1 mm.

have red and brown chromatophores. The red chromatophores fade quickly in preservation and, therefore, are of little use in identification. Comparisons presented here are based on the distribution of brown chromatophores (see also Vecchione 1982).

The number of chromatophores varies considerably between specimens of the same size. The pattern of variability of the most important chromatophore fields are summarized in Figures 4–6.

Several chromatophore groups were found

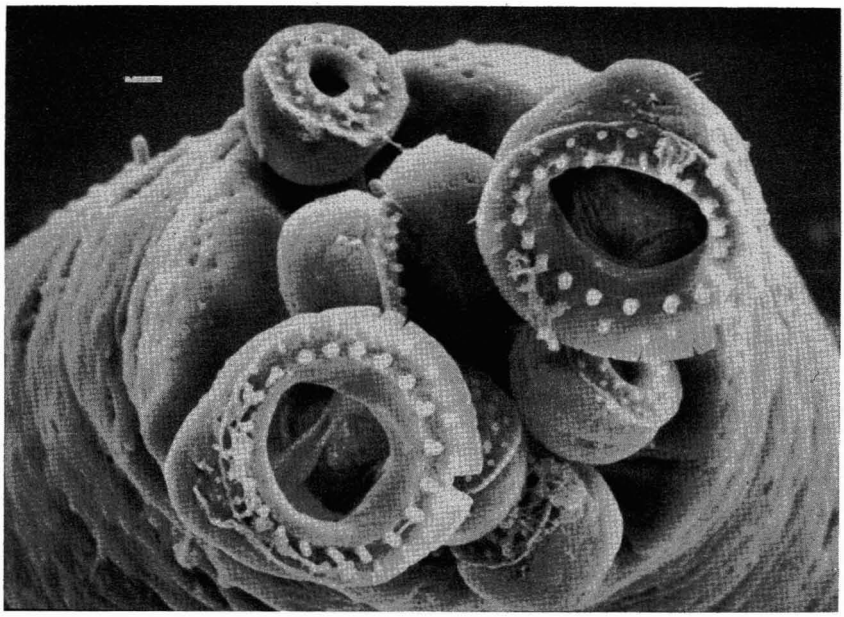

FIGURE 3. Proboscis suckers from a 3.2-mm ML *O. bartramii*. Bar = 10 μm.

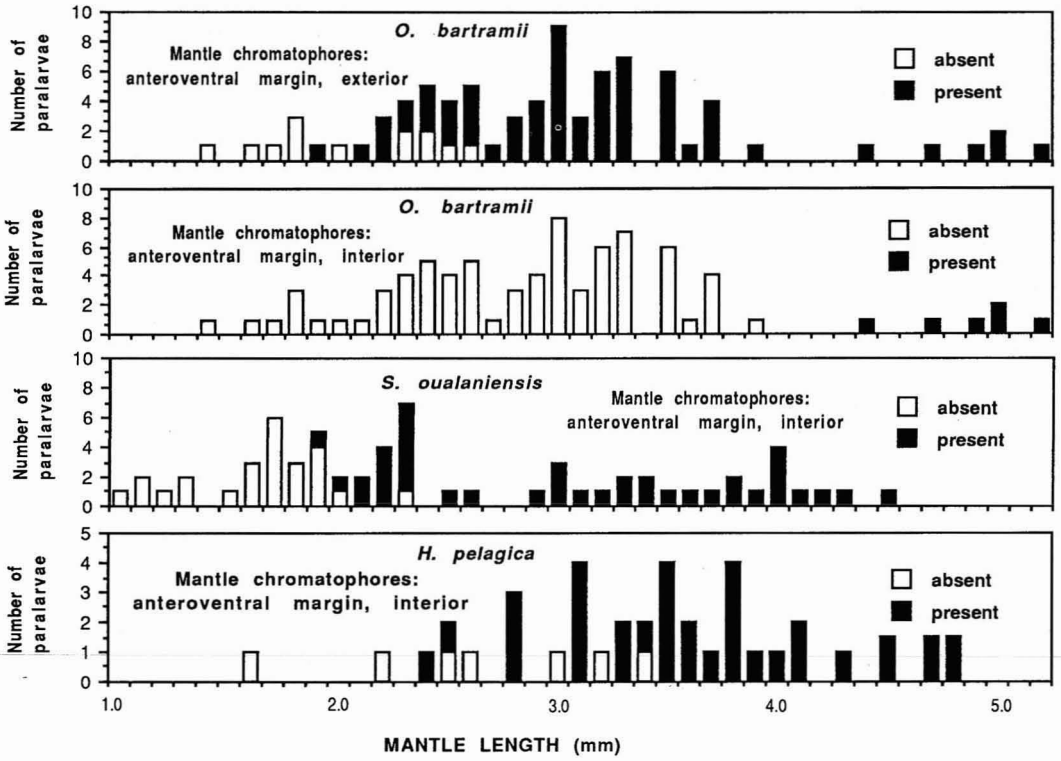

FIGURE 4. Size at which anteroventral mantle chromatophores develop in the three species.

to exhibit specific differences. The exterior chromatophores on the anteroventral mantle margin were unique to *O. bartramii*. These appear in paralarvae between 2.0 and 2.6 mm ML (Figure 4). The interior chromatophores on the anteroventral mantle margin are present in all three species but they develop at different sizes. In *O. bartramii* they develop between about 3.9 and 4.4 mm ML. In *Stenoteuthis oualaniensis* they develop between about 1.8 and 2.3 mm ML, while in *Hyaloteuthis pelagica* they develop between about 2.4 and 3.4 mm ML (Figure 4). There is considerable overlap in the number of posteroventral mantle chromatophores (Figure 5); nevertheless, these can be very useful in identification. *Stenoteuthis oualaniensis* tends to have two or three, *O. bartramii* generally has one or two, and *H. pelagica* usually has one. *Hyaloteuthis pelagica* usually has only one midmantle chromatophore; the other two species have considerably more (Figure 6). Although there is broad overlap in numbers of midmantle chromatophores, there is a tendency for *O. bartramii* to have more than *S. oualaniensis*. One other chromatophore feature clearly separates *H. pelagica* from the other two species. On the dorsal surface of the head, the median anterior and posterior chromatophores are very small compared to the comparable chromatophores in other species (Figure 1). This character is most easily recognized when comparing chromatophores in equal states of contraction. The differences, however, are so great that this character is useful regardless of the states of contraction.

The number of mantle chromatophores undergoes little change from hatching until about 3.5–4.0 mm ML, when chromatophore numbers rapidly increase in all three species (e.g., Figure 6). Diagramatic illustrations of the typical pattern during this early stage for each of the three species are presented in Figure 1.

Chromatophore patterns make identification easy. Unfortunately when damaged specimens lose their chromatophores, other characters must be relied upon. The characters used to separate *H. pelagica* and *S. oualaniensis* have been discussed by Harman and Young (1985). These characters primarily involve the position of photophores and the relative size of the lateral suckers on the proboscis. Unlike those species, *O. bartramii* lacks photophores on the eyes and viscera. The very large lateral proboscis suckers also separate *O. bartramii* from the other two species but not a third Hawaiian species, *Notodarus hawaiiensis*. This latter species, however, has a very different chromatophore pattern as well as a much fatter appearance and shorter proboscis (see Harman and Young 1985).

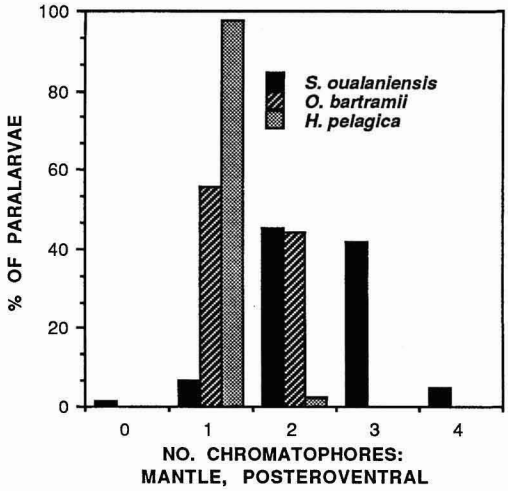

FIGURE 5. Frequency of occurrence of posteroventral chromatophores in paralarvae of the three species.

Distribution

Off Oahu *O. bartramii* paralarvae were captured only during the 22–30 March (1986) and the 8–18 April (1986) NMFS cruises. A time period comparable to the latter was heavily sampled during 7–9 April in 1984, but no *O. bartramii* paralarvae were captured. Neither were any found there on 12–13 April 1979, although in the latter case sampling was minimal.

During the April 1986 cruise off Oahu, 110 *O. bartramii* were captured in 162 oblique tows to 300 m. This compares to 86 *S. oualaniensis* and 64 *H. pelagica*. The "inshore" series during that cruise surprisingly captured *O. bartramii* in about the same numbers as the offshore stations. Mean capture rates were 7.5

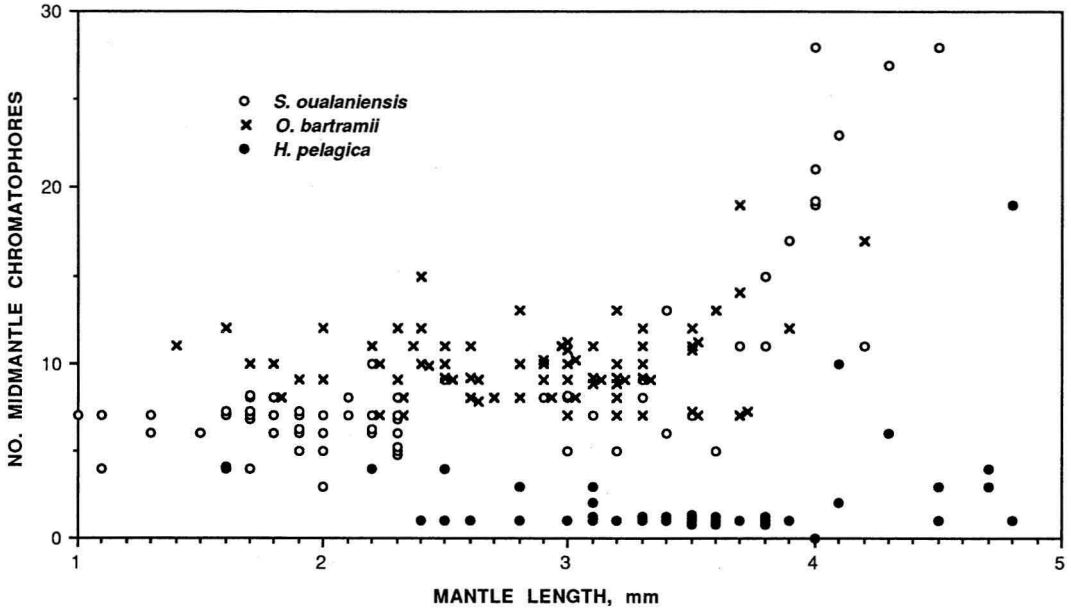

FIGURE 6. Variation in the number of midmantle chromatophores by size in the three species.

versus 6.9 paralarvae per 100 m^2 surface. This contrasts with the strong offshore occurrence of *S. oualaniensis* and *H. pelagica* (mean capture rates per 100 m^2 surface for offshore versus inshore were 8.4 versus 3.5 and 5.3 versus 2.6, respectively). The difference for *S. oualaniensis* (but not for *H. pelagica*) is statistically significant ($P < 0.05$; Mann-Whitney U test).

The data from the series of surface tows suggest that both *O. bartramii* and *S. oualaniensis* were more abundant in surface waters during the day than at night (Figure 7). However, since the sampling represents only one day-night cycle, the data are inconclusive. The changes in hourly abundance of these two ommastrephids show strong covariance, indicating that they were responding to or were affected by similar factors in addition to the day-night cycle, at least during that one period.

The NMFS vertical distribution sampling yielded only 13 *O. bartramii* paralarvae. During the day four were taken in the 0–20-m stratum and four in the 20–40-m stratum. At night three were taken in the 0–20-m stratum and two at the surface. The average abundance was 6.6 paralarvae per 100 m^2 surface. Although the numbers captured were low and the sampling methods differed, the capture rates were comparable between this April (1986) cruise and the preceding March (1986) cruise, suggesting that paralarvae were equally abundant from 22 March to 18 April.

The sampling in April 1979 throughout the archipelago was essentially synoptic. The samples were few in number, however, as they were not designed to capture cephalopod paralarvae. Nevertheless, *O. bartramii* paralarvae were captured at the three most northwestern localities (Figure 8). Off Midway one paralarva was taken in the windward sample. Off Laysan 15 paralarvae were taken in the windward sample (abundance = 89.8/100 m^2) and 1 in the leeward sample, and off French Frigate Shoals 2 were taken in the leeward sample (abundance = 25.8/100 m^2).

DISCUSSION

If we assume that the youngest paralarva of *O. bartramii* taken (yolk present) is less than a week old (from spawning) and that the oldest (separated tentacles) is at least a month old,

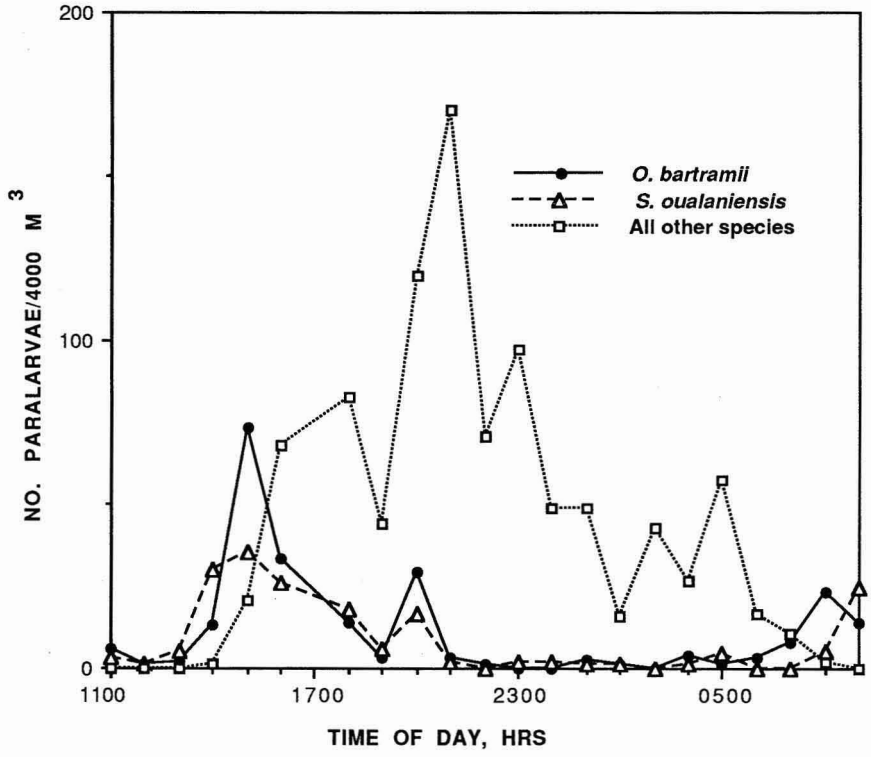

FIGURE 7. Abundance of paralarvae taken in surface tows during one 23-hr period.

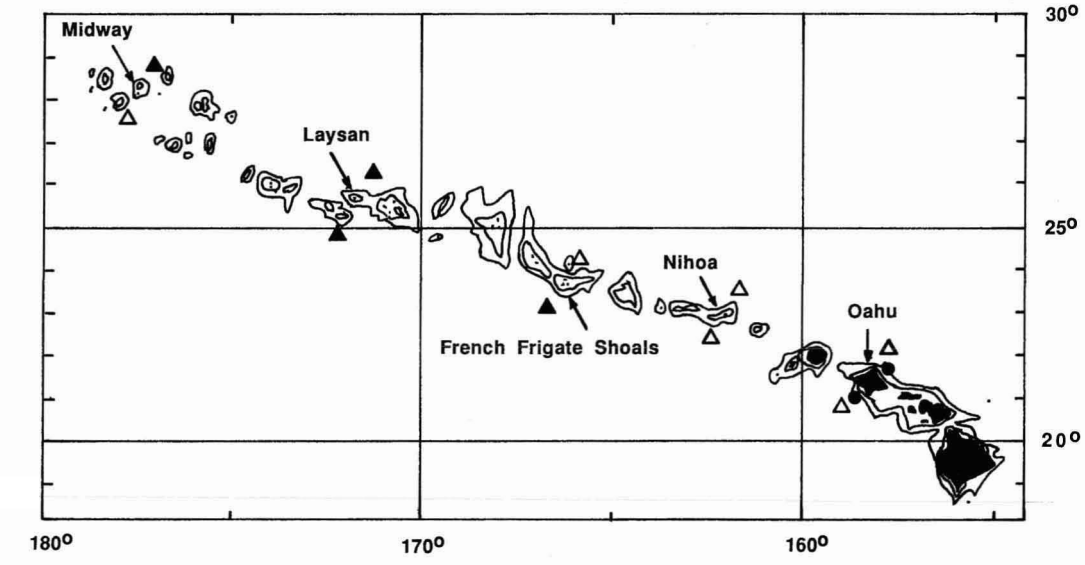

FIGURE 8. Map of the Hawaiian Archipelago showing sampling and capture sites of *Ommastrephes bartramii* paralarvae. Triangles = sample localities for the 1979 survey; filled triangles indicate capture sites. Filled circles = capture sites during 1986.

then we can place the spawning of these paralarvae between late February and early April. The actual spawning period, of course, could be much longer. The absence of paralarvae in our April 1984 and 1979 samples from Oahu suggests either that the squid had a more abbreviated spawning period or that they did not spawn as far south during those years.

The possibility exists that the paralarvae we captured had been advected to island waters from some considerable distance. Assuming, however, that the youngest paralarvae are about 1 week in age from spawning and that net advection during this period amounted to 1.0 km/hr, the spawning site for these paralarvae would be only 168 km away.

Although the plankton series taken along the archipelago in April 1979 had too few tows to draw firm conclusions, they suggest that spawning was more intense along the northwestern half of the archipelago. The capture rates off windward Laysan, if typical, indicate a paralarval abundance over 10 times that off Oahu in March of 1986.

Our data confirm the presence of a second, presumably separate, spawning area for *O. bartramii* in the North Pacific that apparently lies along the islands of the Hawaiian Archipelago. The other area seems to lie somewhere southeast of Japan (i.e., south of 35° N and west of 155° E [Araya 1983]). Araya (1983) suggested that the population of *O. bartramii* west of 165° E rarely interacts with the population east of 170° E. His conclusion was based on patterns of population density and capture-recapture data. The occurrence of spawning along the islands in the Hawaiian Archipelago provides additional support for the possibility that more than one stock of *O. bartramii* exists in the North Pacific.

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